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## Biomass distribution of different-aged needles in young and old *Pinus cembra* trees at highland and lowland sites

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**Abstract** Conifer needles of different ages perform differently in ecophysiology. However, no study has investigated the biomass distribution of different-aged needles in a tree crown or/and a stand canopy. We carried out a study on young (~50 years old) and old (~200 years) *Pinus cembra* L. trees at highland (2100–2300 m a.s.l.) and lowland (570 m) sites in Switzerland. We found that both the young and the old trees living in the highlands had more needle biomass per tree than the same-aged trees of the same species living in the lowlands. This is mainly due to the greater longevity of needles in highland trees. It reflects the strategic responses of trees to low resource availability or high abiotic stress level. Having older needles increases the time that nutrients are resident in trees in less favorable environments, and compensates for shorter growing period in cold temperatures.

**Keywords** Age-dependent · Elevational gradient · Leaf longevity · Needle biomass allocation · Pine

### Introduction

Leaves of most conifers can live for many years. Conifer leaves at different developmental stages (age class) from the apical position (young) to the base (old) on a shoot perform

differently in ecophysiology. Numerous published papers suggested that leaf position and age influence leaf area, gas exchange, leaf conductance, and saturated net photosynthetic rate (e.g. Constable and Ranson 1980; Schoettle 1994; Schoettle and Smith 1999). For instance, young, expanding leaves had lower net photosynthesis (Lieth and Pasian 1990; Schoettle 1994; Araus et al. 1997). Li et al. (2001, 2002) found significant differences in mobile carbohydrate concentrations in different-aged needles of *Pinus cembra* L. trees.

The longevity (the age of the oldest leaves on a branch) of conifer leaves varies from species to species (Mirov 1967; Ewers and Schmid 1981). In *Araucaria* leaves may remain alive for more than 30 years (Elliott 1937). Most other coniferous species bear leaves for much shorter time periods (Molisch 1929). The needle longevity of *Pinus* species is often between 2 and 15 years (Ewers and Schmid 1981). But needles of *Pinus longaeva* may persist on a branch for up to about 45 years (Bailey 1970). However, the intra-specific variation in leaf life span is much less than the inter-specific variation (Eckstein et al. 1999).

The leaf longevity of evergreen conifers such as pine, spruce, and fir increases with increasing elevation and latitude (Weidman 1939; Pravdin 1969; Ewers and Schmid 1981; Reich et al. 1994, 1996). For example, the maximum needle longevity of *Pinus sylvestris* L. doubles from 3 years at 52°N latitude to 7 or more years at 65°N latitude (Pravdin 1969) and the needle longevity of lodgepole pine (*Pinus contorta* Dougl. ssp. *latifolia* Engelm.) was 3.6 years greater at 3200 m elevation than at 2800 m elevation (Schoettle 1990). Similarly, the needle retention in *Picea mariana* (Mill.) BSP varied from 5 to 7 years in the southerly reaches of the boreal forest in Quebec to 13 years in central Alaska and up to 30 years under subarctic conditions (Lamhamedi and Bernier 1994). Field experiments indicate that the mean leaf survival of evergreens may decrease in response to fertilization and irrigation (Shaver 1981; Karlsson 1985; Aerts 1989; Balster and Marshall 2000). Such intra-specific variation in leaf life span is largely explained as an environmentally determined phenotypic acclimation (Reich et al. 1996; Xiao

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2003) and is paralleled by generally decreasing growth rates and photosynthetic capacities of trees in low resource and/or high stress environments (Reich et al. 1992, 1994).

The intra-specific variation of leaf longevity may lead to different needle biomass allocations in trees growing at different sites associated with different environmental conditions. Different-aged needles of conifers affect the gas exchange rate (e.g. Koike et al. 1994; Schoettle 1994; Schoettle and Smith 1999) and carbohydrate content (e.g. Li et al. 2002). In spite of environmental differences, an increase in tree height or age is correlated with a decrease in carbon assimilation rates and stomatal conductance caused by a decline in vascular hydraulic conductance (Yoder et al. 1994; Hubbard et al. 1999). Recently, more stand-growth and yield models have been developed in a carbon balance, process-oriented framework (e.g. Nikinmaa and Hari 1990; Nikolov and Fox 1994). Knowledge of different-aged needle biomass allocation in a tree crown or/and a stand canopy is fundamental to the study of basic exchange processes within the canopy. Estimates of the individual-tree and the stand-level foliage development have been made for many conifer species (e.g. for *P. sylvestris*, Pensa et al. 2001; for *Picea abies* (L.) Karst. and *Larix deciduas* Miller, Li et al. 2003; for *Pinus cembra*, Li and Yang 2004). However, to our knowledge, no study has investigated the biomass distribution of different-aged needles in a tree crown and/or a stand canopy. In other words, no one appears to have addressed the questions of (1) what the distribution pattern is of different-aged needles within a crown of a juvenile and/or an adult tree, as well as in the canopy of a stand and (2) whether trees growing at high elevations have more needle biomass per tree than the same species with the same age at low elevations, due to the greater needle longevity at high elevations. To answer these questions we carried out a study of young ( $\sim 50$  years old) and old ( $\sim 200$  years) *P. cembra* trees at highland (2100–2300 m a.s.l., alpine tree-line ecotone) and lowland (570 m a.s.l.) sites in Switzerland. The highland trees emerged from natural regeneration, whereas the lowland trees were planted in garden. Reich et al. (1996) studied the needle longevity of common-garden-grown lowland populations of *P. sylvestris* (16 populations) originating from a wide latitudinal range ( $47^{\circ}$ – $60^{\circ}$ N) and *P. abies* (18 populations) from a wide elevational origin (670–1235 m elevation). They concluded that the longer leaf longevity of populations in low-temperature habitats at high elevations and high latitudes is not the result of genotypic variation, but an environmentally regulated phenotypic acclimation. This finding meant that we could study the biomass distribution of different-aged needles in highland and lowland *P. cembra* trees regardless of their origin.

## Material and methods

### Highland site

The highland site is located within the natural climatic treeline ecotone at Mont Noble ( $46^{\circ}12'N$ ,  $7^{\circ}30'E$ ), Canton

Valais, Swiss Central Alps. The test trees (*P. cembra*) were grown between 2100 and 2300 m a.s.l., on a steep NW-facing slope of  $\sim 30^{\circ}$ . Soils belong to the acid rendzina type on calcareous bedrock, with a ground cover dominated by *Vaccinium myrtillus* L., *Empetrum hermaphroditum* (Lange) Hagerup, *Arctostaphylos alpina* (L.) Sprengel, *Loiseleuria procumbens* (L.) Desv., *Cladonia* spp., *Cetraria islandica*. The root zone temperature at 10 cm depth averages about  $6.5^{\circ}C$  during the growing period ( $\sim 4$  months from June to September). The mean air temperature of the warmest month (July) is around  $10^{\circ}C$ . The mean precipitation is  $\sim 630$  mm per year, with most of this amount falling during the growing season.

### Lowland site

The lowland *P. cembra* trees sampled were grown in Birmsdorf ( $47^{\circ}21'N$ ,  $8^{\circ}31'E$ ; 570 m a.s.l.), Canton Zurich. The site was garden ground without fertilizer in the past. The weakly acid brown soils were densely covered by a ground vegetation layer dominated by *Poa* spp., *Luzula* spp., *Carex* spp. etc. The annual mean air temperature at the site is  $8.2^{\circ}C$ . The mean temperature of the warmest month (July) is  $15.7^{\circ}C$  and of the coldest month (January) is  $-7^{\circ}C$  (data from 1963 to 1985). The mean precipitation is 1,111 mm per year (data from 1961 to 2003) with most of this amount falling during the growing season ( $\sim 7$  months from April to October).

### Sampling

Samples were taken at the end of the growth period at both sites, i.e. on October 20, 2003 at the highland site and on October 26, 2003 at the lowland site.

In this study, the young trees were  $\sim 5$  m in height and 7–10 cm in diameter and the old ones were  $\sim 15$  m in height and 30–40 cm in diameter. At the highland site, we selected six young and six old *P. cembra* trees, but at the lowland site only four young and three old ones were selected due to lack of trees. Only healthy and undamaged trees were used.

The crown of each selected tree was divided into three equal parts with an upper, middle and lower section. One NW-oriented (referring to the NW-facing slope at the highland site) mean branch was taken from the middle of each section per selected tree, i.e. three branches were collected from each tree. We used only healthy and undamaged branches that had intact terminal buds.

Throughout this paper “branch” is defined as an axis that directly originates from the main stem of the tree. A “shoot” originates directly from the main axis of a branch or from an older shoot. The foliage of a branch is supported on different-aged needles of the main axis and on variedly aged needles of the attached shoots. “Age class” refers to both branch (shoot) segments and needles that are firmly attached to the stem of a branch/shoot. Although we sampled after the 2003 growing season, but still in 2003 (October),

**Table 1** Needle biomass (kg) per age class and the total needle biomass (kg) in old and young *P. cembra* trees growing in the highlands (2100–2300 m a.s.l.) and the lowlands (570 m) in Switzerland

| Needle age           | Current year  | 1 year        | 2 years       | 3 years      | 4 years      | >4 years | Total <sup>a</sup> |
|----------------------|---------------|---------------|---------------|--------------|--------------|----------|--------------------|
| Old lowland trees    | 9.298 ± 1.14  | 5.555 ± 1.25  | +             | +            | +            |          | 14.853             |
| Young lowland trees  | 2.016 ± 0.42  | 1.292 ± 0.47  | 0.311 ± 0.06  | +            | +            |          | 3.619              |
| Old highland trees   | 18.745 ± 2.32 | 16.213 ± 2.08 | 12.227 ± 1.17 | 5.656 ± 1.01 | 1.023 ± 0.04 | +        | 53.864             |
| Young highland trees | 2.304 ± 0.37  | 1.887 ± 0.24  | 1.295 ± 0.35  | 0.400 ± 0.04 | 0.084 ± 0.01 | +        | 5.970              |

Values are mean ± SD;  $n = 6$  for the young and old highland trees each;  $n = 4$  and  $n = 3$  for the young and old lowland trees, respectively. “+” in the table means that few needles still remained

<sup>a</sup>Total needle biomass (kg) of a tree crown

the 2003 year needles are named as current year needles. Correspondingly, current year branch or shoot segments means 2003 year branch/shoot segments. One-year-old branch (shoot) segments means the segments emerged in 2002. The pine dwarf shoots can be fairly accurately dated by counting back the internodes or age classes of the dwarf shoots from the stem tip (cf. Kozłowski 1971). In the present study, the age of needles and shoot segments in each selected branch was determined using marks from overwintering buds on the stem and by counting annual needle cohorts.

Needles and shoot segments (including rhytidome) were separately collected according to the age class of the needles and branches/shoots for each collected branch. The collected needles and shoot segments were dried to a constant weight at 70°C and weighed. The needle biomass of each age class and the total needle biomass of a tree (crown) were estimated using the needle biomass of these three sampled branches multiplied by the sum of the branches for each section. Using the Winrhizo software (Regent Instruments Inc.), leaf area was scanned and analyzed (Genenger et al. 2003). Afterwards the needle dry mass (70°C, 3 days) was determined and the leaf mass per unit area (LMA,  $\text{g m}^{-2}$  as the ratio of leaf dry mass to projected leaf area) was calculated.

The leaf longevity was registered using the collected branch from the lower section because only branches old enough to have at least an oldest segment (close to the main stem of the tree) lacking leaves can be used to record the needle longevity. The annual branch increment was also measured on the branch collected from the lower crown section in each tree. The annual branch increment is defined as the apical growth of the stem (main axis) that was added each year to the branch.

### Data analysis

All data were averaged from each tree age category (old trees and young trees) at each site (highland and lowland). A two-factor (two elevations × two tree age categories;  $\alpha = 0.05$ ) Anova (Microsoft Excel 2000) was used to compare LMA and the means of the total biomass of needles (and foliated shoot segments) per tree and to test for an interaction between these two factors. *T*-test ( $\alpha = 0.05$ ;

Microsoft Excel 2000) was conducted for other statistical significance analysis.

## Results

### Leaf longevity

The leaf longevity of the highland *P. cembra* trees was 2–3 years more than that of the lowland ones (see Table 1 also). The age of the oldest needles of *P. cembra* growing in the highlands was 5 years, whereas the leaf longevity of the same species in the lowlands was 2 years and rarely reached 3 years (Table 1).

### Leaf mass per unit area (LMA)

There were no significant interaction effects between elevation and tree age on LMA and there were no significant differences in the means of LMA between young and old trees or between highland site and lowland site. For both tree age categories the highland trees have slight but non-significant greater LMA than the lowland trees (Table 2). Both at the highland site and at the lowland site, old trees showed slight but nonsignificant higher LMA than that of young trees, and old needles have slight but nonsignificant greater LMA than that of the current year needles (Table 2). LMA of young trees growing at the highland site exceeded that at the lowland site by 4.4% for current year needles (214.59 for young highland trees vs. 205.50 for young lowland trees) and by 2.1% for 1-year-old needles (218.12 vs. 213.68). Similarly, LMA of old trees growing at the highland site exceeded that at the lowland site by 4.9% for current year needles (223.41 for the old highland trees vs. 212.88 for the old lowland trees) and by 3.2% for 1-year-old needles (227.90 vs. 220.73). At the highland site, LMA of the old trees exceeded that of the young trees by 4.1% for current year needles (223.41 for old trees vs. 214.59 for young trees) and by 4.5% for 1-year-old needles (227.90 vs. 218.12). Similarly, at the lowland site, LMA of the old trees exceeded that of the young trees by 3.6% for current year needles (212.88 for old trees vs. 205.50 for young trees) and by 3.3% for 1-year-old needles (220.73 vs. 213.68).

**Table 2** Leaf mass per unit area (LMA, g m<sup>-2</sup>) of old and young *P. cembra* trees growing in the highlands (2100–2300 m a.s.l.) and the lowlands (570 m) in Switzerland

|                      | Highland       |                | Lowland        |                |
|----------------------|----------------|----------------|----------------|----------------|
|                      | Young trees    | Old trees      | Young trees    | Old trees      |
| Current year needles | 214.59 ± 2.61  | 223.41 ± 15.23 | 205.50 ± 13.61 | 212.88 ± 15.39 |
| 1-year-old needles   | 218.12 ± 6.70  | 227.90 ± 14.46 | 213.68 ± 10.52 | 220.73 ± 18.67 |
| 2-year-old needles   | 221.41 ± 26.26 | 222.53 ± 16.63 | No needles     | No needles     |
| 3-year-old needles   | 218.90 ± 5.17  | 225.32 ± 10.07 | No needles     | No needles     |
| 4-year-old needles   | 215.98 ± 18.61 | 223.52 ± 7.40  | No needles     | No needles     |

Values are mean ± SD; *n* = 6 for the young and old highland trees each; *n* = 4 and *n* = 3 for the young and old lowland trees, respectively

### Needle biomass distribution in a tree crown

The trees had different needle biomass according to their age (young vs. old) and location (highland vs. lowland), which were related to the different site conditions (Table 1). The mean total needle biomass per tree significantly differ by tree age (old tree > young tree; *p* = 0.0006), by elevation (highland tree > lowland tree; *p* = 0.0002), and the interaction between elevation and tree age is also significant (*p* = 0.0064). The different longevity of the needles led to different total needle biomass in the crowns of the same-aged trees grown at different sites (highland site vs. lowland site; Table 1). The total needle biomass of a young lowland tree was only 61% (3.619 kg) of that of a young highland tree (5.970 kg). Even an old lowland tree had only 28% (14.853 kg) of the total needle biomass of an old highland tree (53.864 kg; Table 1).

All the trees apart from the old lowland trees (i.e. the young lowland trees and the young and old highland trees) showed a similar vertical needle biomass distribution in the three sections within a tree crown. The maximum needle biomass for the old lowland trees was in the mid-section, whereas the maximum needle biomass for the others was in the bottom crown section and progressively decreased from the bottom to the middle and then to the top section.

### Different-aged needle biomass fraction

The different-aged needle biomass fraction of the total needle biomass in a tree varied between the lowland trees (only three age classes, i.e. current year to 2-year-old needles) and the highland ones (where there were five classes with current year to 4-year-old needles) (Fig. 1).

Trees at both sites followed a similar pattern of development with respect to the relative shares of needle biomass per age class, i.e. the needle biomass fraction per age class tended to decrease with increasing needle age (Fig. 1). The trees in the lowlands had a greater biomass fraction of current year and 1-year-old needles than those in the highlands because the lowland trees lacked older needles (Fig. 1). The old lowland trees had the greatest biomass fraction (62.6%) of current year needles, whereas the old highland trees had the smallest biomass fraction (34.8%) of current year needles. The fraction differentiation (7%) in the means of current year needles between old (62.6%) and young trees (55.7%) in the lowlands was not statistically significant

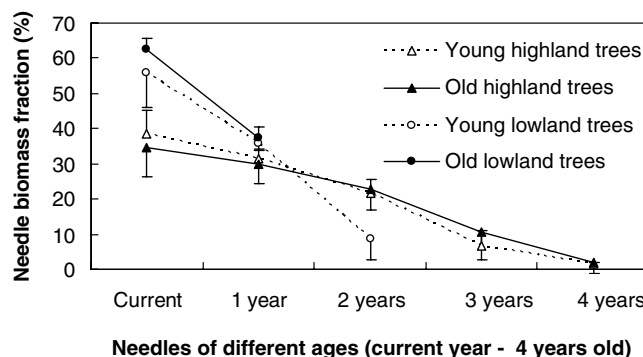
(*p* = 0.34). Similarly, the fraction differentiation in the means of the current year needles (4%) between the old trees (34.8%) and the young trees (38.6%) in the highlands was not statistically significant (*p* = 0.56) and nor was that of the 3-year-old needles (old trees = 10.5%; young trees 6.7%; *p* = 0.13; Fig. 1). This means that no differences in the needle biomass fraction per age class could be detected between the young and the old trees at either the highland or the lowland sites.

### Needle biomass per branch

The total needle biomass per branch sampled in the lower crown section differed in the old and young trees at both the highland and lowland sites. In the young tree category, a branch in a highland tree had a needle biomass of 191 (± 26) g, whereas a branch in a lowland tree had a significantly (*p* = 0.0043) lower (– 34%) needle biomass (127 ± 18 g). Similarly, in the category of old trees, a branch in a highland tree had a needle biomass of 396 (± 94) g and a branch in a lowland tree had a significantly (*p* = 0.0176) lower (– 57%) needle biomass (171 ± 34 g).

## Discussion

The characteristics of conifer leaves (e.g. leaf longevity and physiology) are responsive to microenvironmental



**Fig. 1** Different-aged needle biomass fraction (%) of the total needle biomass of young and old *P. cembra* growing in the highlands (2,100–2,300 m a.s.l.) and lowlands (570 m) in Switzerland (*n* = 6 for the young and old highland trees each; *n* = 4 and *n* = 3 for the young and old lowland trees, respectively). For the sake of clarity, “+ SD” and “– SD” are used



**Table 3** The  $p$ -values from significance tests ( $T$ -test,  $\alpha = 0.05$ ) for the differences in the means (needle length; annual increment of leading branch) between the old and young *P. cembra* trees growing

in the highlands (2100–2300 m a.s.l.) and the lowlands (570 m) in Switzerland

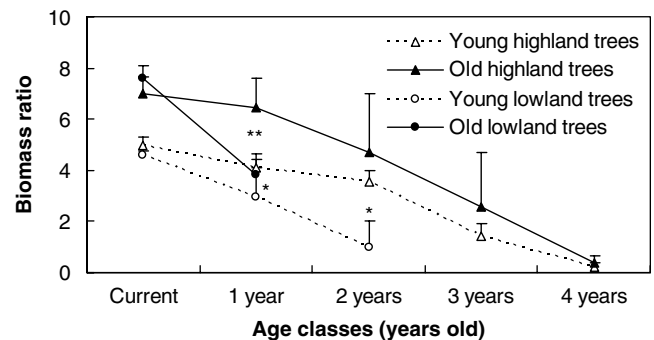
|                     | Young highland trees |        |                 |        | Old highland trees |        |                 |        |
|---------------------|----------------------|--------|-----------------|--------|--------------------|--------|-----------------|--------|
|                     | Needles              |        | Branch segments |        | Needles            |        | Branch segments |        |
|                     | Current year         | 1 year | Current year    | 1 year | Current year       | 1 year | Current year    | 1 year |
| Young lowland trees | 0.30                 | 0.41   | 0.04            | 0.03   |                    |        |                 |        |
| Old lowland trees   |                      |        |                 |        | 0.19               | 0.18   | 0.45            | 0.89   |

variables within a crown (e.g. young leaves vs. old leaves; Whitney 1982; Schoettle and Smith 1991), site nutrient (Brix 1981; Turner and Olson 1986) and water availability (Kozłowski 1976), elevation (Weidman 1939; Ewers and Schmid 1981; Schoettle 1990, 1994) and latitude (Pravdin 1969). Elevation has a strong influence on radiation, temperature, evaporation, wind speed and snow accumulation, as well as on soil erosion and transport, local water balance, etc. (Aulitzky 1963; Barry 1981). In other words, elevation seems to be a substitute for the complexity of local environmental elements on a given aspect (Li et al. 2003; Li and Yang 2004). Hence, the leaf life span in highland *P. cembra* trees was 2–3 years more than that in lowland ones. Such a phenomenon has been found in *Pinus* species (e.g. Schoettle 1990; Nebel and Matile 1992; Jalkanen et al. 1995; Warren and Adams 2000; Lamppu and Huttunen 2001; Pensa and Sellin 2002; Xiao 2003) and in many other species (Kudo 1991, 1996; Karlsson 1992; Lamhamedi and Bernier 1994; Reich et al. 1996, 1999). For instance, the needle longevity of *P. cembra* increased with increasing altitude (Nebel and Matile 1992) and decreased by 1–3 years on the east-facing slope compared to the north-facing slope at the same elevation in Switzerland (Koike et al. 1994). In *P. tabulaeformis* Carr., Xiao (2003) found that needle longevity significantly increased with latitude ( $p < 0.0001$ ) and decreased with mean January temperature ( $p < 0.0001$ ) in NW-China (cf. Schoettle and Rochelle 2000). Ewers and Schmid (1981) reviewed the literature data for 37 species of *Pinus* native to the United States and Canada and field data for eight taxa (21 populations) of pines growing at various elevations in California and found a significantly positive correlation between elevation and needle longevity in each case. However, Pouttu and Dobbartin (2000) did not find any statistically significant differences in needle longevity in old *P. sylvestris* trees grown along an elevational gradient (550–1380 m) in Valais, Switzerland, proposing that summer drought and strong radiation at high elevations strongly affected the needle longevity.

It is well-known that plant species in nutrient-poor habitats have thicker or tougher (more sclerophyllous) leaves than those occurring in more resource-rich habitats (Chapin 1980; Fonseca et al. 2000). Consequently, the highland trees showed greater LMA compared with the lowland trees (cf. Wright et al. 2002). Both the greater longevity and the greater LMA of needles in trees growing in the highlands may result, as we found, in more needle biomass per tree at high elevations compared with the trees of the same species and same age at low elevations. Our study revealed that both the young and the old trees living in the highlands

had more needle biomass per tree than the same-aged trees of the same species living in the lowlands (see question 2 in the “Introduction” section). Moreover, such a finding may also be due to other factors, for example, (1) the annual increment of branches/shoots (longer the branches, more the needles), (2) the density of needles attached to the branch or shoot per unit length (more density, more needles), and (3) the length (mass) of a single needle. We found, however, no statistically significant difference in needle length and in branch growth elsewhere, except for the annual increment of branches between the young highland trees and the young lowland trees (lowland trees > highland trees;  $p < 0.05$ ; Table 3). Moreover, the old lowland trees had a significantly ( $p = 0.009$ ) lower biomass ratio of 1-year-old needles to 1-year-old branch segments than the old highland trees (Fig. 2). Similarly, the young lowland trees also had significantly lower biomass ratios of 1-year-old needles to 1-year-old branch segments ( $p = 0.039$ ) and of 2-year-old needles to 2-year-old branch segments ( $p = 0.013$ ) than the young highland trees (Fig. 2). This indicates that part of the 1-year-old needles of the lowland trees (both young and old) had already shed which finally led to shorter leaf longevity and lower total needle biomass per tree in the lowlands (shorter needle longevity, less total needle biomass).

Individuals of *P. cembra* in the alpine treeline ecotone are often found isolated from their neighbors and show a stunted morphology with a wide green-crown. Like the total needle biomass of a tree, we found that a branch in the highland trees had more needle biomass than one



**Fig. 2** Biomass ratio (+ SD) of needles to branch segments per age class in young and old *P. cembra* growing in the highlands (2,100–2,300 m a.s.l.) and lowlands (570 m) in Switzerland ( $n = 6$  for the young and old highland trees each;  $n = 4$  and  $n = 3$  for the young and old lowland trees, respectively). Asterisks indicate significant differences (\* $p < 0.05$ , \*\* $p < 0.01$ )

in the lowland trees for each tree age category (young or old trees). Schoettle (1990) found that leaf longevity was greater (+ 3.6 years) on shoots in trees (*P. contorta* Dougl. ssp. *latifolia* Engelm.) growing at 3,200 m (13.1 years) than at 2800 m elevation (9.5 years). However, she did not find that the increased leaf longevity in the lodgepole pine at high elevations (3200 m a.s.l.) resulted in increased foliar biomass per shoot above the values measured on the shoots at low elevations (2,800 m). Her findings may result from the less annual increment of the shoot growth in trees at 3200 m (− 33%) compared with those at 2,800 m (shorter branch, less needle biomass). Although we found significant decrease in apical growth of many tree species with increasing elevation (Tranquillini 1979; Li et al. 2003; Li and Yang 2004), we did not find any statistical difference in annual branch growth between old trees growing in the highlands and the lowlands, but significant differences in that between young trees growing in the highlands and the lowlands (lowland trees > highland trees;  $p < 0.05$ ; Table 3). This suggests that once trees/stands are tall enough (> 3 m) to create a forest microclimate, the topography related to the local climate determines growth, as Li et al. (2003) and Li and Yang (2004) described. The same needle biomass did not lead to the same growth rate of branches in the case of Schoettle (1990). Similarly, Bernoulli and Körner (1999) found that the tree height declined with increasing elevation but not the total tree biomass. One reason for this is that chilling temperatures may contribute to retarded growth at higher elevations, as Körner (1998) proposed in a paper on tree growth at the treeline. However, Koike et al. (1994) found a negative correlation between maximum photosynthesis and needle life span of *P. cembra* trees at the alpine treeline in the Swiss Alps, which may partly explain why the longer leaf longevity and more needle biomass in highland trees did not cause greater branch growth rate than in lowland trees in our study (cf. Tranquillini 1979). The younger needles would significantly contribute to the total carbon gain of a tree, because younger needles have better capacities for carbon gain due to their spatial distribution for light capture in a tree crown and their better assimilation properties compared to the older ones as they may have a carbon balance close to zero, even negative, due to shading. Hence, the inner and lower needles which are shaded fall on the ground at an earlier stage and only the physiologically active young needles are left (Table 1, Fig. 1). This may be a successful strategy for high carbon acquisition to maintain a higher growth rate for trees growing at favorable sites in the lowlands (Li et al. 2003; Li and Yang 2004).

It seems clear that the biomass distribution of needles is different in the highland and lowland trees (see question 1 in the “Introduction” section) because they have different age classes of needles in the tree crowns (more age classes, more needles). Surprisingly, both in the lowlands and the highlands, there was no statistical difference in needle biomass fraction per age class between the old and the young trees (Fig. 1), i.e. the needle biomass fraction did not seem to depend upon tree age but rather on site conditions.

## Conclusions

Our analysis shows that the longer leaf longevity and the greater total needle biomass in trees growing in the highlands are environmentally dependent (cf. Reich et al. 1996), i.e. these differences reflect the strategic responses of the trees to low resource availability and/or high abiotic stress level. In less favorable environments it may be a successful strategy to increase the time that nutrients are resident in the trees. Moreover, it may also be a successful mechanism to compensate for shorter growing season at high elevations or/and latitudes (4 months in highlands vs. 7 months in lowlands in this study). Since leaf age and mass related to gas exchange influence both ecological processes and the carbon balance (cf. Li et al. 2001, 2002; Xie and Luo 2003), our findings suggest that large scale process-oriented forest models (e.g. with respect to carbon balance) should try to take into account through intelligent upscaling approaches both the process-related information (e.g. needle biomass) and the structural information (e.g. biomass distribution pattern of different-aged needles) of different-aged forest stands growing in different site conditions.

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## References

- Aerts R (1989) The effect of increased nutrient availability on leaf turnover and aboveground productivity of two evergreen ericaceous shrubs. *Oecologia* 78:115–120
- Araus JL, Amaro T, Zuhair Y, Nachit MM (1997) Effect of leaf structure and water status on carbon isotope discrimination in field-grown durum wheat. *Plant Cell Environ* 20:1484–1494
- Aulitzky H (1963) Grundlagen und Anwendung des vorläufigen Wind-Schnee-Ökogrammes. Mitt. Forstl. Bundes-Vers.anst. Wien 60:763–834
- Bailey DK (1970) Phytogeography and taxonomy of *Pinus* subsection *Balfourianae*. *Ann Missouri Bot Gard* 57:210–249
- Balster NJ, Marshall JD (2000) Decreased needle longevity of fertilized Douglas-fir and grand fir in the northern Rockies. *Tree Physiol* 20:1191–1197
- Barry RG (1981) Mountain weather and climate. Methuen, London, New York
- Bernoulli M, Körner C (1999) Dry matter allocation in treeline trees. *Phyton* 39:7–12
- Brix H (1981) Effects of thinning and nitrogen fertilization on branch and foliage production in Douglas-fir. *Can J For Res* 11:502–571
- Chapin FS (1980) The mineral nutrition of wild plants. *Annu Rev Ecol Syst* 11:233–260
- Constable GA, Ranson HM (1980) Effect of leaf position, expansion and age on photosynthesis, transpiration and water use of cotton. *Aust J Plant Physiol* 7:89–100
- Eckstein RL, Karlsson PS, Weih M (1999) Research review: Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate-arctic regions. *New Phytol* 143:177–189

- Elliott JH (1937) The development of the vascular system in evergreen leaves more than one year old. *Ann Bot NS* 1:107–127
- Ewers F, Schmid R (1981) Longevity of needle fascicles of *Pinus longaeva* (Bristlecone pine) and other North American pines. *Oecologia* 51:107–115
- Fonseca CR, Overton JM, Collins B, Westoby M (2000) Shifts in trait combinations along rainfall and phosphorus gradients. *J Ecol* 88:964–977
- Genenger M, Zimmermann S, Hallenbarter D, Landolt W, Frossard E, Brunner I (2003) Fine root growth and element concentrations of Norway spruce as affected by wood ash and liquid fertilisation. *Plant Soil* 255:253–264
- Hubbard RM, Bond BJ, Ryan MG (1999) Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiol* 19:165–172
- Jalkanen R, Aalto T, Kurkela T (1995) Development of needle retention in Scots pine (*Pinus sylvestris*) in 1957–1991 in northern and southern Finland. *Trees* 10:125–133
- Karlsson PS (1985) Effects of water and mineral nutrient supply on a deciduous and an evergreen dwarf shrub: *Vaccinium uliginosum* L. and *V. vitis-idaea* L. Holarctic. *Ecology* 8:1–8
- Karlsson PS (1992) Leaf longevity in evergreen shrubs: variation within and among European species. *Oecologia* 91:346–349
- Koike T, Häslér R, Item H (1994) Needle longevity and photosynthetic performance in cembran pine and Norway spruce growing on the north- and east-facing slopes at the timberline of Stillberg in the Swiss Alps. In: Schmidt WC, Holtmeier, Proceedings International workshop on subalpine stone pines and their environment: the status of our knowledge. FK (eds), Gen Tech Rep INT-GTR-309. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, pp 78–80
- Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115:445–459
- Kozlowski TT (1971) Growth and development of trees, vol 1. Academic Press, New York
- Kozlowski TT (1976) Water supply and leaf shedding. In: Kozlowski TT (ed) Water deficits and plant growth, vol. IV. Academic Press, New York, pp 191–231
- Kudo G (1991) Effect of snow-free duration on leaf life-span of four alpine plant species. *Can J Bot* 70:1684–1688
- Kudo G (1996) Intraspecific variation of leaf traits in several deciduous species in relation to length of growing season. *Ecoscience* 3:483–489
- Lamhamedi MS, Bernier PY (1994) Ecophysiology and field performance of black spruce (*Picea mariana*): a review. *Ann Sci For* 51:529–551
- Lamppu J, Huttunen S (2001) Scots pine needle longevity and gradation of needle shedding along pollution gradients. *Can J For Res* 31:261–267
- Li MH, Hoch G, Körner C (2001) Spatial variability of mobile carbohydrates within *Pinus cembra* trees at the alpine treeline. *Phyton* 41:203–213
- Li MH, Hoch G, Körner C (2002) Source/sink removal affects mobile carbohydrates in *Pinus cembra* at the Swiss treeline. *Trees* 16:331–337
- Li MH, Yang J (2004) Effects of microsite on growth of *Pinus cembra* in the subalpine zone of the Austrian Alps. *Ann For Sci* 61:319–325
- Li MH, Yang J, Kräuchi N (2003) Growth responses of *Picea abies* and *Larix decidua* to elevation in subalpine areas of Tyrol, Austria. *Can J For Res* 33:653–662
- Lieth JH, Pasian CC (1990) A model for photosynthesis of rose leaves as a function of photosynthetically active radiation, leaf temperature, and leaf age. *J Am Soc Hort Sci* 115:486–491
- Mirov NT (1967) The genus *Pinus*. Ronald Press Co., New York
- Molisch H (1929) Die Lebensdauer der Pflanze. Fischer, Jena
- Nebel B, Matile P (1992) Longevity and senescence of needles in *Pinus cembra* L. *Trees* 6:156–161
- Nikinmaa E, Hari P (1990) A simplified partitioning model for Scots pine to address the effects of altered needle longevity and nutrient uptake on stand development. In: Dixon PK, Meldahl RS, Ruark GA, Warren WG (eds) Process modeling of forest growth responses to environmental stress. Timber Press, Portland, Oregon, pp 263–270
- Nikolov NT, Fox DG (1994) A coupled carbon-water-energy-vegetation model to assess responses of temperate forest ecosystems to changes in climate and atmospheric CO<sub>2</sub>. Part I. Model concept. *Environ Pollut* 83:251–262
- Pensa M, Jalkanen R, Sellin A (2001) Age-dependent changes in needle-fascicle dynamics of *Pinus sylvestris* (L.). *Scand J For Res* 16:379–384
- Pensa M, Sellin A (2002) Needle longevity of Scots pine in relation to foliar nitrogen content, specific leaf area, and shoot growth in different forest types. *Can J For Res* 32:1225–1231
- Pouttu A, Dobbartin M (2000) Needle-retention and density patterns in *Pinus sylvestris* in the Rhone Valley of Switzerland: comparing results of the needle-trace method with visual defoliation assessment. *Can J For Res* 30:1973–1982
- Pravdin LF (1969) Scots pine: variation, intraspecific taxonomy and selection. *Academija Nauk SSSR (Moskva)*, 1964. Translated from Russian by Israel Program for Scientific Translation, Jerusalem
- Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD (1999) Generality of leaf trait relationships: A test across six biomes. *Ecology* 80:1955–1969
- Reich PB, Koike T, Gower ST, Schoettle AW (1994) Causes and consequences of variation in conifer leaf life span. In: Smith WK, Hinckley TM (eds) Ecophysiology of coniferous forests. Academic Press, San Diego, pp 225–254
- Reich PB, Oleksyn J, Modrzynski J, Tjoelker MG (1996) Evidence that longer needle retention of spruce and pine populations at high elevations and high latitudes is largely a phenotypic response. *Tree Physiol* 16:643–647
- Reich PB, Walters MB, Ellsworth DS (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol Monogr* 62:365–392
- Schoettle AW (1990) The interaction between leaf longevity and shoot growth and foliar biomass per shoot in *Pinus contorta* at two elevations. *Tree Physiol* 7:209–214
- Schoettle AW (1994) Influence of tree size on shoot structure and physiology of *Pinus contorta* and *Pinus aristata*. *Tree Physiol* 14:1055–1068
- Schoettle AW, Rochelle SG (2000) Morphological variation of *Pinus flexilis* (Pinaceae), a bird-dispersed pine, across a range of elevations. *Am J Bot* 87:1797–1806
- Schoettle AW, Smith WK (1991) Interrelation between shoot characteristics and solar irradiance in the crown of *Pinus contorta* ssp. *latifolia*. *Tree Physiol* 9:245–254
- Schoettle AW, Smith WK (1999) Interrelationships among light, photosynthesis and nitrogen in the crown of mature *Pinus contorta* ssp. *latifolia*. *Tree Physiol* 19:13–22
- Shaver GR (1981) Mineral nutrition and leaf longevity in an evergreen shrub, *Ledum palustre* ssp. *decumbens*. *Oecologia* 49:362–365
- Tranquillini W (1979) Physiological Ecology of the Alpine Timberline: Tree existence at high altitudes with special references to the European Alps. Ecological Studies, Vol 31. Springer-Verlag, Berlin Heidelberg New York, pp 1–137
- Turner J, Olson PR (1986) Nitrogen relations in a Douglas-fir plantation. *Ann Bot* 40:1185–1193
- Warren CR, Adams MA (2000) Trade-offs between the persistence of foliage and productivity in *Pinus* species. *Oecologia* 124:487–494
- Weidman RH (1939) Evidences of racial influence in a 25-year test of ponderosa pine. *J Agric Res* 59:855–887
- Whitney GG (1982) A demographic analysis of the leaves of open and shade grown *Pinus strobes* L. and *Tsuga canadensis* (L.) Carr. *New Phytol* 90:447–453

- Wright IJ, Westoby M, Reich PB (2002) Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *J Ecol* 90:534–543
- Xiao Y (2003) Variation in needle longevity of *Pinus tabulaeformis* forests at different geographic scales. *Tree Physiol* 23:463–471
- Xie S, Luo X (2003) Effect of leaf position and age on anatomical structure, photosynthesis, stomatal conductance and transpiration of Asian pear. *Bot Bull Acad Sin* 44:297–303
- Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR (1994) Evidence of reduced photosynthetic rates in old trees. *For Sci* 40:513–527